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PRINCIPLES OF PLANT TAXONOMY, X*.

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In previous papers the remarkable fact has been presented that the entire plant kingdom as it exists today is made up of seven progressive stages or subkingdoms with definite transition gaps of greater or less extent between them. The whole series is the result of a building up process, the higher emerging from the lower throughout the entire system. The gaps do not represent breaks in the evolutionary progression but simply the aquisition of new potentialities with a greater or less elimination of groups of plants in the transition condition from one cause or another. In some cases the geological record has supplied important missing links in others no definite transition types whatever have so far been uncovered.

In some quarters, there has been a tendency to use these breaks in the general continuity in support of fantastic evolutionary theories which would give new starting points for the various isolated groups practically all along the geological history. The fact of the non-conformity in the geological formations is supposed by some to give plausibility to the notion that there were many independent transitions from the non-living to the living. Such notions are not only fantastic but greatly increase the difficulties they would remove.

It is just in those regions of the general progressive series where the evolutionary movement compels a decided change in external life relations that the great breaks occur. Of the six transitions within the present taxonomic system of plants two, the first and the fourth, present no very great hiatus even though the new potentialities added are very effective in determining new modes of biological reactions and processes.

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At the appearance of sex, with the initiation of fertilization and reduction, a profound change is brought about in the method of hereditary transmission, namely Mendelian heredity, which is added to the previous mode of purely nonsexual propagation. In the fourth transition, where the time of sex determination is shifted to the sporophyte, and new biological relations are established, including decided sex dimorphisms and dimorphic reactions in various parts of the bisporangiate or monecious individual, there is also only a slight break in the continuity of forms in the various phyla which pass through this change. On the other hand, the remaining transitions involved readjustments to ecological relations and here the destruction of forms, judging from the size of the gaps, has been very great.

The great transition from the Thallophyta to the Metathallophyta involves the passage from aquatic life to a properly adjusted aerial life and also the establishment of one generation as a parasite on the other. In the transition to the vascular plants the ecological change involved is from a completely parasitic condition to a two-phased condition of the sporophyte, the parasitic juvenile phase of the individual changing gradually to an independent mature phase which finally evolves roots and prominent leaves. In the transition to the seed condition the ecological changes are again very great involving the complete parasitism of the gametophyte on the mature sporophyte, the establishment of a two-phased male gametophyte, and the intercalation of a resting phase between the parasitic and independent phases of the sporophyte. This necessitates the acquirement of very rapid readjustment reactions during the sprouting period, along with numerous other minor changes. It is no wonder that plants evolving through this progression were destroyed by the wholesale as they encountered the oscillating changes of climate and earth level during the geological ages. The transition of both the Gymnosperms and Angiosperms was from a Heterosporous Pteridophyte condition. The transition to the Angiosperms is not, properly speaking, a transition from Gymnosperms to Angiosperms but only a transition of a much greater extent and much greater advance from lower forms than that which took place in relation to the Gymnosperms. The most important change, involving ecological readjustment, was the closing of the megasporophyll, making necessary a new organ, the stigma, for the process of pollination. The closing of the sporophyll is in evidence in

various degrees in some Ferns, but in these there was no serious ecological relation involved as in the Angiosperms. In the Angiosperms not only must pollination be accomplished through a new organ, as compared with the gymnospermous condition, but the pollen tube must be readjusted to a new ecological relation, commonly involving growth through an open cavity, and, of course, growth of a much greater extent than is necessary in the Gymnosperms. These new ecological relations are probably largely responsible for the great hiatus separating our present day Angiospermæ from their nearest possible, living relatives, the Eusporangiate Ferns.

Any careful study of the taxonomic system, immediately emphasizes the remarkable fact of the great similarity and uniformity running through the whole extent of both the plant and animal series and the remarkable similarity of fundamental characteristics and properties possessed in common by the highest forms in contrast to their dissimilarity to the lowest organisms, like the lower Blue-green Algæ and Bacteria. Taking an inventory of the more important similarities exhibited by the highest plants and the highest animals, we get the following:

1. They both have essentially similar cell organization.
2. They both have the same general type of cell division (karyokinesis).
3. They both begin life as single cells.
4. They both develop into enormous, multicellular aggregates.
5. They both have differentiation systems of cells, tissues, and organs.
6. They both have sex potentiality.
7. They both have primary sexual states, causing attraction.
8. They both have essentially similar dimorphic gametes, or heterogamy.
9. They both have secondary sexual states with secondary sexual dimorphism.
10. They both produce a unitary reproductive cell from two independent units (fertilization), thus developing as diploid organisms.
11. They both have a synapsis of homologous chromosomes, resulting in a definite segregation (reduction division).
12. In consequence of fertilization and reduction, they both show fundamentally similar hereditary phenomena, namely Mendelian heredity, involving the phenomena of dominance and recessiveness and proportionate segregation of characters after hybridization.

13. They both show a general adaptation to an aerial life and dry land habitat while at the same time betraying vestigial characters indicating an evolution out of an aquatic condition.
14. They both have a parasitic interrelation of offspring to parent, the offspring developing within the protective confines of the parent.
15. They both have sperm cells which are not deposited into the water, as in lower sexual forms, but into the ovary or a special cavity of the female.
16. They both provide a food supply in one way or another to assist the offspring in establishing an independent life after the parasitic connection is broken.
17. In both the higher animals and plants there is a very decided and abrupt change from the parasitic connection to the independent life, the embryonic individual very quickly developing entirely new reactions and functions not in evidence before.
18. In the unisexual species, they both show a greater or less supply of vestigial structures of the opposite sex, indicating an evolution from a former hermaphroditic condition and the same mode of determinate orthogenetic evolution of the time of sex determination in the life cycle.
19. They both show definite correlation reactions throughout the organism as a whole together with the development of definite functional gradients.
20. They both show stability in the more fundamental group characteristics and frequently instability in small specific differences.

This array of similarities and others that might be enumerated show that the entire organic kingdom is a unit and has had a common starting point and an essentially similar mode of evolution. The lowest organisms known lack all of the things given above with the exception of a partial realization of the first characteristic and a slight evidence of the last one. As stated, since we have these profound biological parallelisms between such extreme phylogenetic lines as the highest plants and the highest animals we are impelled to accept the view of a single common origin if we are to maintain an evolutionary principle on a basis of logic and common sense rather than on a foundation of anarchistic reasoning.

The great hiatuses are then to be interpreted as breaks in the survival series rather than as breaks in the uniform continuity of the organic evolutionary process; and we may then proceed to fill out the great gaps as best we can with theoretical and fossil forms.

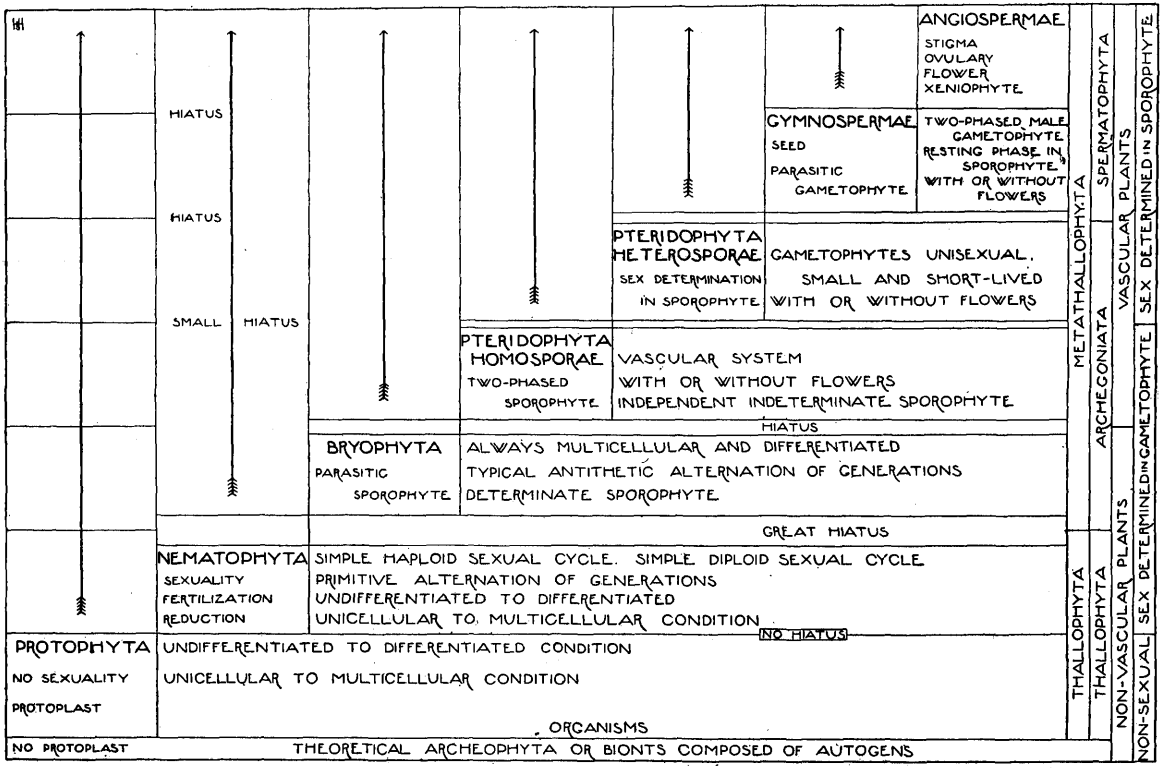

Chart showing the seven fundamental divisions or subkingdoms of living plants and the way the fundamental system is built up by the addition of potentialities to those already present.

THE TRANSITION FROM THE NON-LIVING TO THE LIVING.

We think of a time when the earth was without living beings. Non-living matter ordinarily consists of atoms and molecules, of crystals, and of coloidal particles. These, however do not show any of the distinctive qualities of life. Life is a property of protoplasm, and protoplasm consists of coloidal particles in water. In passing from the non-living to the living we are passing from the unorganized to a biologically organized system. The ultimate particles of the living system are self-perpetuating coloidal particles. The essential, ultimate living particles must have the following properties:

1. They must be autonomous or self-perpetuating, taking dead matter and reorganizing this into their own peculiar pattern with their own peculiar properties. These ultimate units are appropriately called *autogens*.
2. They must have the power of self-division after attaining a certain size, and this division is an equational division leaving the two resulting, daughter particles with the same potentialities as the original.
3. They must have the power of correlative interaction so that a number of these ultimate living units are held together in a limited or unitary reaction field.
4. They must have the power or property of intermittent mutation, by which, in isolated cases, a new pattern in one or more of the ultimate biological units or autogens is produced.

Aggregates of one or more types of these autogens would then constitute the primitive bionts, and there may have been an evolutionary series leading up to the lowest known organisms or lowest protoplasts as we have them at present in the autophytic Bacteria. Are there any such bionts, below the organization stage of the simplest protoplasts, in the world at present? Are there "species" which form an ascending ladder toward our simplest organized protoplasts (organisms)? Are disease producing plant viruses of such a nature? If these are bionts, then they need a special technique and method for their study which is neither chemical nor biological as this term applies to organized protoplasts, extending from the lowest known Bacteria to the highest plants and animals. If certain viruses are parasitic bionts, then we would expect them to pass into the contracted dry condition or spore-like state like many of the higher protoplasts and, with the return of favorable moisture and other conditions, to return to the active plasma state.

The viruses appear not to be able to perpetuate themselves except as parasites and saprophytes. This condition could not have been the beginning, as intimated above. No claim as to the nature of viruses is made here. They may be only enzymes, they may be bionts, or they may be organisms. Or known viruses might perhaps come into each of these categories. The problem however of the disease-producing viruses seems to be a problem for the cytologist primarily.

If there really are such pre-cellular bionts in existence, they would fall into the first of the ten divisions or subkingdoms of plants evolved during the geological ages and would be true Archeophyta.

Theoretically, in dealing with any sort of abiogenesis, we come sooner or later face to face with the problem of organization, if we believe in evolution at all. What is it that causes an evolution of organization, first of the protoplast itself as the unit (for there is an ascending scale from the lower Bacteria to the well organized protoplasts of all the Metaphyta). and second an evolution in the unitary reaction system of the multicellular individual?

THE TRANSITION TO THE SEXUAL, MULTICELLULAR, DIFFERENTIATED ORGANISMS.

In passing from the Protophyta to the Nematophyta, there is a broad transition belt with no prominent break in the continuity. Three fundamental potentialities arise, two of which are to be seen in their primordial evolutionary stage in the higher Protophyta. We have the evolution of the sex potentiality, the evolution of the multicellular condition, and the evolution of differentiation systems. These three do not appear in the same sequence in the various phyla and classes; so the sex potentiality is taken as the most important characteristic to segregate the first two subkingdoms, the Protophyta and the Nematophyta. The evolution of the multicellular condition and of differentiation is simply the accumulation of various hereditary potentialities which in themselves have no great consequence at the time of their several introductions. But with the introduction of the sex potentiality, which is probably the result of an advanced organization of the protoplast and especially of the nucleus, a profound change takes place in the reaction system of the entire life cycle, giving rise to the dimorphic development of the gametes with attractive

properties, resulting in fusion into a unitary system from the two independent units, and to a synapsis of chromosomes at a later period followed by reduction. As a consequence of these two processes, the Mendelian method of hereditary transmissions and interactions is established.

The change from the nonsexual to the sexual apparently was accomplished independently in various phyletic lines and was not dependent either on the multicellular condition or on the presence of vegetative differentiation potentialities. Its appearance was dependent on causes having their origin in the peculiar structure of living matter of a certain degree and type of complexity.

THE TRANSITION BETWEEN THE NEMATOPHYTA AND THE BRYOPHYTA.

The greatest hiatus in the entire plant series occurs between the Nematophyta and the Bryophyta. There is little probability that any recognizable missing links will ever be found in the fossil record to help fill the gap. For geologically these plants evolved long before the paleozoic era. It is practically certain that none have survived to the present day. It is expedient, therefore, to construct a series of hypothetical forms. In the first place the ancestors must have been filamentous green Algæ. The prominent protonema of the Bryophyta and its presence in the lower Pteridophyta fully justify such an assumption. Then this filamentous group gradually built up a multicellular constitution retaining the more primitive potentialities to be active in the juvenile part of the ontogenetic gradient. Sooner or later, with the introduction of solid tissues, plurilocular gametangia were established which by simple, direct transformations evolved into the archegonia and antheridia of the lower Bryophyta. Unicellular and multicellular rhizoids also were probably evolved before the transition and transformation to aerial conditions. The Phaeosporæ have plurilocular gametangia, but the liverworts and mosses evidently did not evolve from the Brown Algæ. They have too many special peculiarities. In a very early stage a normal alternation of generations was established which soon advanced to the typical antithetic type with a completely parasitic diploid sporophyte. No living green Alga has such a cycle. In fact it is not present in any of the living Algæ. One can see that a large number of funda-

mental morphological and ecological progressions was necessary to bring the procession up to even the lowest bryophyte stage.

Theoretically then, the great hiatus between the Nematophyta and the Bryophyta must be represented by hypothetical forms that were evolving at the same time as the higher Nematophyta. If there were any surviving representatives they would constitute a distinct and important division of the plant kingdom and would appropriately be called Protobryophyta.

THE TRANSITION FROM THE BRYOPHYTA TO THE PTERIDOPHYTA HOMOSPORÆ.

There is a large break between the Bryophytes and Pteridophytes but not nearly so great as that between the Nematophytes and Bryophytes. In this transition, the geological record gives some information and no doubt will disclose many more transition links in the future.

The main advances are as follows:

1. Change from a determinate sporophyte to an indeterminate one.
2. Change from a permanently parasitic sporophyte to an independent mature condition, only the juvenile stage being parasitic.
3. Gradual shifting of the point of origin of the sporangium from the simple terminal bud to a lateral appendage, namely the leaf.
4. Change from determinate death with the end of the reproductive process in the sporophyte, to indefinite long-continued existence not affected by the reproductive process.
5. Change from an unbranched system to a sporophyte either with dichotomous or monopodial branching.
6. Development of a vascular system and in some lines of a cambium layer.
7. Development of roots.
8. Development of leaves.
9. Reduction of the gametophyte.
10. Sinking of the archegonium venter into the tissue of the thallus, or rather recession of the differentiation reaction into the earlier stages of the ontogeny, resulting in a sunken venter with only the archegonial neck differentiating from the archegonial outgrowth.

There is no direct connection with any of the higher Bryophytes although the Anthocerotæ with their sunken archegonial venter are a closely related parallel series. We must then postulate a bryophyte ancestor with a reducing gametophyte, with sunken venter, with a tendency to enlarge the sporophyte into a

more efficient reaction system and with a definite progressive tendency to shift the reproductive tissue from the center of the axis to the outside. Since the lower Pteridophyta usually have a rather well-developed protonemal stage they are reasonably derived from the same ancestral stock, namely the green Algæ, as the Bryophytes. They passed through the bryophyte stage and were probably already segregated into the various phyletic groups long before they progressed to the present advanced position of even the lowest living Ferns. Two main phyletic lines, at least, are in evidence, the fern line with the evolution of an original cylinder of open vascular bundles and cambium, and a lepidophyte line with a more closed vascular strand, as in our present Lycopods, although these might also have had a more open bundle system until they were definitely specialized into our modern types.

As to the order in which the various pteridophyte mutations appeared, one can only guess, because of so little fossil evidence accumulated up to the present. There may have been different sequences in the several phyletic lines. The essentials, of course, were the initiation of a branching ability, the lateral movement of the spore-producing areas with accompanying indeterminateness and independence of the mature sporophyte, and the evolution of leaves and roots from the terminal gowing bud. If efficiency of meristematic growth and dichotomous branching were established before the sprangium had traveled to the margin of the stem or onto a leaf appendage, then there might be continuous vegetative growth in some axes even though others were definitely determinate because of the continuance in the race of a bryophyte type of terminal sporangium. Psilophyton appears to have been a decidedly intermediate plant, fitting into the theoretical series necessary for passing from a bryophyte stage to the lycopod condition. Psilophytons apparently were plants with vigorous growth and dichotomous branching, with no definite leaves and perhaps without roots. They still had large terminal sporangia like a moss or liverwort and these, of course, would end the growth of any branches which produced them, but other branches could continue the vegetative growth. *Rhynia gwynne-vaughani* appears to have been an even more primitive plant of the same series. It apparently had terminal cauline sporangia, vigorous growth as compared with any known bryophyte sporophyte, and dichotomous branching but no roots or leaves. Such leafless branch-

ing fossil species with large terminal sporangia are not to be compared with Algæ but with bryophyte sporophytes. Such a comparison indicates four important advances beyond the bryophyte condition as follows: (1), The evolution of long-continued, vigorous growth; (2), the acquirement of an independent mature phase of the sporophyte with the development of a rhizome-like base which could probably act as an absorbing organ; (3), a dichotomous branching system; (4), A dimorphic reaction in the terminal buds so that some developed terminal sporangia like the Bryophytes and some continued the vegetative growth.

There is no definite evidence that the fern series was derived from the lycopod line. The evidence is rather in the opposite direction. The most reasonable assumption, if the Lycopods cannot be derived from ancestral Ferns, is that both types of vascular systems were derived from a moss-like central strand of the primitive stem. Campbell has shown that there is a very direct connection between the Ophioglossales and a bryophyte ancestor something like Anthoceros. The embryology is decidedly bryophyte-like; the first leaf, stem tip and root all coming from the outer segment of the egg. Whatever the ancestral type of the lepidophyte vascular system may have been, we know that it shows the same disposition to scatter in some of the higher Selaginellas as do the bundle systems in the Leptosporangiate Ferns, Monocotyls, and various small groups of Dicotyls. It is becoming evident that at least all the vascular systems of the living plants except perhaps those of the Lepidophyta had their origin from the primitive fern type, namely the circle of open bundles with a cambium cylinder as in the Ophioglossales.

The hiatus between the Bryophytes and the Homosporous Pteridophytes represents a transition which must have contained a large number of groups in a lower stage of evolution than our present Lycopods and Ferns. Rhynia and Psilophyton represent transition forms between the Lycopodiaceæ and their bryophyte ancestors while no ancestral Ferns of the same level are known at present. But fern-like ancestral forms with terminal and perhaps lateral cauline sporangia must have existed. The fern series never evolved a dichotomous branching system and the ancestral groups must either have had unbranched but vigorous sporophytes with an independent mature phase or else they were evolving a rudimentary monopo-

dial branching potentiality. All such plants whether ancestral Lycopods or Ferns were the true Protopteridophyta.

The lowest vascular plants in which the sporangia had traveled from a terminal position to a lateral position on a lateral appendage or leaf probably had alternating zones of sporophylls and foilage leaves just as soon as indeterminate growth was fully established as is the case in all flowerless fern types and in the typical flowerless living Lycopods. For it is a general characteristic of primitive ontogenies to have rhythmical repetitive reactions rather than irregular sequences. Such rhythmical reactions depending on developing gradients, are seen not only in the alternation of zones of sporophylls and foliage leaves but also in the rhythmical appearance of branches or branch whorls on the main stem alternating with branchless zones, as in Araucaria and other Conifers and some species of Magnolia. Any species then which was thrown from the juvenile vegetative condition with foliage leaves to a permanent condition of sporophyll production, until the stopping of growth of the reproductive branches was attained, would indicate a first slight movement toward definite strobilus or flower evolution. In the most primitive condition the sporangia would not be on the leaves but directly on the axis, so systems could develop in which small leaf whorls would alternate with whorls or zones of sporangia.

THE TRANSITION FROM HOMOSPOROUS TO HETEROSPOROUS PLANTS.

For some unknown reason, after the sporophyte has attained a certain degree of advancement in the various phyletic lines, the point of sex determination passes from gametophyte to sporophyte. The general reason is that the orthogenetic progression can continue until the zygote is reached, and this progression is in evidence in many higher phyletic series. The movement is a process in which the time of sex determination continues to gain on the ontogeny until the determinate limit is reached in the fertilized egg or zygote where this evolutionary advancement necessarily comes to an end in the attainment of diecious species. The fact must be emphasized that the transition from sex determination in the haploid gametophyte to the diploid sporophyte is not dependent on the simple or double number of chromosomes nor to any special kind of morphology. It took place in series that had the lepidophyte

morphology as well as in series that had the ptenophyte and calamophyte morphology. It took place without reference as to whether a flower had evolved in the system or not. There was a great destruction of forms of plants which had arrived at this stage of evolution. But this is not to be ascribed to the change in sex condition but rather to the increasing helplessness of the gametophyte which at this stage went hand in hand with the evolutionary progression in the time of sex determination. Some of the missing links leading from the Homosporous Ferns to the Cycads have been discovered, namely the Pteridospermæ, but not much progress has been made in uncovering missing links which must have been left behind on the path leading up to the Strobilophyta. There are also very few fossil links known which might aid in solving the problem of the vast isolation of the Anthophyta.

THE TRANSITION TO THE GYMNOSPERMS.

The great advance which culminated in the perfection of the seed was certainly one of the major events in the evolution of organisms. The main movements were, of course, the making of a complete parasite out of the gametophyte; the gradual intercalation of a resting phase, often followed by a long period of dormancy, between the parasitic embryonic phase and the independent mature phase of the sporophyte; and the two-phased parasitic growth of the pollentube. Each of these changes required decided ecological adjustments. The lower Cycadophyta are flowerless plants, like the Ferns, with simple rosettes of sporophylls, while most of the advanced forms attained to the strobilus stage, acquiring a definite, determinate, reproductive axis, as is prominently shown in the higher Cycadeæ. In the Ginkgo series, however, no flower was evolved, although the other important morphological systems advanced to a very high condition. The gymnosperm strobilus is of the same general nature as that which appeared in the Lycopodium and Equisetum lines. It is perfectly evident that the flower had a large number of independent origins, just like the origin of heterospory or various other important, orthogenetic, evolutionary advances, as for example the development of dimorphism between sporophylls and foliage leaves and the attainment of dieciousness. In all the various cases, however, the evolutionary process was the same; namely, the introduction of a determinate potentiality active in the reproductive shoot and

the continued movement of this potentiality toward a more definite reaction and a more prompt determination in relation to the ontogenetic gradient of the floral axis.

The primitive types of flowers are represented in Lycopodium, Equisetum, Selaginella, Cycadeoidea, Encephalartos, Araucaria, Magnolia, Ranunculus, and Echinodorus. Extreme types are present in Taxus, Gnetum, Naias, Typha, Wolffia, Corallorrhiza, Monolepis, Peperomia, Casuarina, Salix, Hippuris, Xanthium, and Taraxacum. The attempt to evolve a flower from an inflorescence must be regarded as fantastic and based on anarchistic modes of thought. If one takes an inventory of the acquirements of complex systems of potentialities possessed by the entire plant, namely the complete compliment of hereditary factors, of any of the extreme types mentioned above, it will be found that the species with reduced flowers have the most complex reaction systems, and that in them the various evolutionary progressions which have been operative from the beginning are also the most advanced in the species which have the most extreme flowers. The various evolutionary movements, although they are mainly independent of each other, show a remarkably consistent, forward progression.

When one makes a study of such a classification as that developed in the Engler system or the proposals put forth by Wettstein and others, where a Magnolia, for example, with its decidedly simple and rhythmical reaction system, is derived from the Gnetales, with their enormous complement of extreme specializations, and evolved through such forms as Casuarina, Quercus, Juglans, etc., or their immediate theoretical ancestors, then the whole scheme appears not only fantastic but the extreme of absurdity.

In the lower Homosporous Pteridophytes there were no doubt series evolved with alternating simple zones or whorls of sporophylls and foliage leaves, or in some cases with lateral cauline sporangia subtended by foliage leaves or bracts. One would expect such types from the fact that the spore-producing activity travels out from the center of the primary stem to the leaf appendages and in some cases even to the epidermis of the leaves; and after a branching system had evolved it often is shifted entirely away from the primary axis to secondary or tertiary axes and their appendages. These special, primitive systems present in some fossil plants give no excuse for pre-

tending to see a reducing, branched inflorescence when the evolution of branching whether dichotomous or monopodial had hardly begun.

The Strobilophyta are much more isolated from the Pteridophyta than the Cycadophyta but not nearly so much as are the Anthophyta. The general evolutionary movements are the same as in the Cycadophyta, only on a more advanced and complex scale. The Araucariales are plainly the most primitive conifers, and from the lowest broad-leaf Araucariaceæ the evolution of the leaf is consistently carried forward to the extremely reduced scale and needle-leaf types. The flower also evolved consistently in the same direction and along with it there is a parallel advance of numerous other characteristics.

Conifers show no evidence of a previous, bisporangiate condition of the flower. But in all three orders, Araucariales, Pinales, and Taxales, both monecious and diecious species are present. Although the movement in the evolution to unisexuality is not closely associated with or dependent on any other evolutionary advance taking place in the plant body, yet there is sometimes a parallelism of evoluting movements as would be expected if evolution is progressing in definite directions. In the Pinales dieciousness is only attained in the most extreme genus, Juniperus, some species of this genus still being monecious and some diecious. In the Taxales which show a consistently higher level in nearly all evolutionary movements, dieciousness is attained quite a number of times in independent genera.

The problem of connecting the Conifers with the Ptenophyta is to find fossil missing links, especially Heterosperous Ferns, but the question arises as to whether these would be recognized as ancestral Conifers even if discovered. The connecting links would be broad-leaved (not necessarily compound) trees; the line finally extending below the level of the presence of flowers and probably of branches.

In passing downard to theoretical ancestors, two conditions are possible for a derivation of monecious and diecious flowers as represented by present Conifers. Differential gradients determining one or the other sexual states in any reproductive bud may have been established before the mutation to determine reproductive axes took place, just as we have monecious flower systems in which one or the other sex condition is temporarily established in the primary axis from which the secondary

floral axes branch off. Then with the introduction of reproductive determinateness monosporangiate flowers would naturally follow directly. On the other hand, undiscovered bisporangiate flowers may have preceded the monosporangiate condition, which would lead back to indeterminate reproductive zones with one sexual state present at the beginning stage of development, and through a sex reversal, with the opposite sexual state at the end of the ontogeny of the reproductive zone. Then the introduction of reproductive determinateness would necessarily give bisporangiate flowers. The lack of vestigial structures of the opposite sporophylls is against this hypothesis and would indicate that the conifers never had bisporangiate flowers. The same reasoning may be applied to the living Cycadales in spite of the fact that their relatives, the Bennettitales, had bisporangiate flowers.

The Gneteæ, on the other hand, like many monecious and diecious Angiosperms, plainly had ancestors with bisporangiate flowers, since some of them show definite vestigial structures of the opposite set of sporophylls.

THE TRANSITION TO THE ANGIOSPERMÆ.

As stated previously, the Angiosperms or Anthophyta, did not have their origin in any of the living groups of Gymnosperms. At most the nearest approach to a common ancestry of the two groups might be sought in hypothetical Heterosporous Pteridophytes which would trace back to Eusporangiate Ferns, where both open and closed vascular bundles evolved, comparable to the open and closed bundles of the Dicotyls and Monocotyls. In various Leptosporangiate Ferns there is a strong tendency to close up the leaflets of the sporophylls. This attains extreme development in the Marsileales. Now we will have to assume that somewhere along the line the ancestral Angiosperms passed from the open to the closed megasporophyll. Since the stamens were apparently not involved in the movement it probably did not occur until the group was passing through the Heterosporous Pteridophyte stage or to the seed-bearing condition.

If there were already distinct phyletic lines of ancestral Angiosperms established, then all the lines passed through the same progression. And this is the usual occurrence in all fundamental evolutionary movements. When it comes to general growth habit and form, many of the Monocotyl trees

are much nearer the primitive Fern type than any Dicotyls and there is no special reason for supposing that they did not come through the last three subkingdom stages in substantially the same form.

The vascular system of the Monocotyls probably segregated off long before one could speak of Monocotyls and Dicotyls in the modern sense. The same movement developed to a slight extent in many lines of Dicotyls giving scattered and partially closed vascular bundles in many, mostly decidedly advanced Dicotyl groups. Thus, so far as the vascular system is concerned, the "Monocotyls" probably evolved from the "Dicotyls." But when it comes to embryonic structures the evolution was plainly in the opposite direction. The primitive Ferns have one "cotyledon" and the Monocotyls have simply continued this condition, with various minor modifications, while the Dicotyl embryo represents a decided specialization which also appeared, probably independently, in the Cycadophyta and Strobilophyta. The Dicotyl type of embryo advanced in specialization in various Strobilophyta until a whorl of numerous cotyledons was attained. On the other hand, the Dicotyl type of embryo may be transformed into a "Monocotyl" type by the introduction of a factor which suppresses one member, as in Claytonia. The notion that the Monocotyl condition was derived from the Dicotyl by fusion is to be considered only as a survival of an archaic method of morphological reasoning which thought of the plant as being built up of distinct parts rather than as developing through the reaction of hereditary potentialities which were successively evolved and through which the reaction system is changed at the right point in the ontogenetic cycle provided a proper environment is at hand. We know that a change to a suitable environment will often cause a new reaction and bring out structures which never could have appeared in the normal sequence of the phylogenetic history.

The flowers of the Angiosperms are plainly and conclusively strobili, as stated above, of the same general nature as those of Equisetum, Lycopodium, Dioon, and Araucaria. They are determinate, reproductive axes with ordinary, modified sporophylls. They were all of a single primary bisporangiate type originally and the indication is that they evolved about the time when heterospory was attained. From the bisporangiate condition they advanced to the various degrees of moneciousness

and dieciousness while at the same time a general evolutionary movement was going on producing a more definite and an earlier action of the determinate potentiality. That the primitive Angiosperms were entomophilous without special adaptations is hardly open to question. Various Ferns, like *Pteris aquilina* for example, have abundant nectaries on their leaves and these are visited by various insects which gather the abundant secretions while the leaves are expanding. No one at present would continue to put forth the foolish teleological claim that such visits were a life and death advantage to the plant or any advantage at all. Some of the Angiosperms had the nectaries from the beginning and some perhaps did not. The presence of an insect environment could not determine the origin of nectaries, although in the presence of an insect environment specializations may evolve which will cause elimination whenever this special insect environment is absent.

With the introduction of branching potentialities and reductions, inflorescences were finally evolved which are of the same general nature and due to the same causes as the inflorescences one finds in the higher Lycopods, in some of the Taxodiaceæ, and in the Gneteæ. The development of a perianth and of a peduncle is again of the same general nature as the development of peduncles or perianths in Equisetum or of peduncles and specialized basal sporophylls in certain Lepidophyta, Cycadophyta, and Strobilophyta. The Angiosperms, developing a definite bisporangiate condition, with the stamens below, obtained a perianth mainly by the transformation of stamens. As special potentialities were added that came into play mainly when the ontogenetic gradient was passing through the zone from vegetative determination to reproductive determination in the flower, the stage was set for special developments on this transition zone, resulting in peduncles and perianths. Neither the Engler system nor Wettstein's speculations can be taken seriously by any one who has advanced along modern lines of discarding teleological evolutionary theories and who thinks of evolution as an orderly mutative process, to account for the taxonomic system; for this system shows the most remarkable orderliness not only in the great fundamental progressions from the most simple to the most complex organisms but also in the sequences of the subordinate phyla and smaller series.

When the claim is made that the Magnolia flower represents the primitive type of flower for all Angiosperms, we are not claiming an immediate monophyletic origin of all existing Angiosperms, except in the broadest sense, any more than when we claim that the strobilus of a Lycopod and the strobilus of a Cycad are exactly homologous structures do we intimate that these two diverse groups had an immediate monophyletic origin. The Protangiosperms must have been evolving as a distinct phylum side by side with the Gymnosperms and at the same time.

There is but one rational view in respect to the evolution and phylogeny of the Anthophyta. They connect with the lower members of the great mother phylum of all the living seed plants, namely with the Ptenophyta. They evolved strobili of the same general nature as the Equisetaceæ, the higher species of Lycopodium, the Selaginellaceæ, the Cycadaceæ and the lower Coniferæ. The lowest living Angiosperms, as stated above, still have these strobilus-like flowers with very moderate modifications, in fact with modifications so slight that one can make a direct comparison with the strobili of Homosporous Pteridophytes. These flowers, in fact all flowers, consist of a main determinate axis bearing sporophylls. In some cases modified sporophylls appear even in very low types; in others there is a direct succession to the foliage leaves below. The flowers are derived from indeterminate axes through mutative processes which involve the development of functional gradients, these gradients not being subject to rejuvenation or repetition normally as in the lower stage where rosettes or zones of sporophylls alternate with the growth of vegetative leaves. The retention of the primitive condition is represented among living higher plants in the carpellate rosettes of Cycas and the carpellate and staminate rosettes on the indeterminate dwarf branches of Ginkgo. From the primitive strobilus type of flower have evolved all the diversified flower types in both Angiosperms and Gymnosperms and the sequence to the extremes can easily be followed out in a host of phylogenetic lines. The evolution resolves itself into a few simple, fundamental movements which were practically the same in all the series.

The botanist who deserves credit above all others for laying the foundation of modern plant phylogeny on a correct and rational basis was Dr. Charles E. Bessey and the writer has

often marveled that those who were supposed to have some intimate knowledge of systematic botany, both in America and Europe, could not see the way after it had been pointed out by Bessey, but persisted in phylogenetic speculations and taxonomic arrangements which make a travesty of any rational notion of plant evolution whatever. When the series are in proper order we discover a remarkable system and the actual movements of the evolutionary process become evident. With improper arrangements, like some which are still in high repute and in very general use, the whole system appears hap-hazard and the product of the whims of witches rather than of a rational order of law. One can be sure, however, that the disorder is in the minds of the taxonomists and not in the plant system itself.

I am greatly indebted to Dr. Lois Lampe for the execution of the accompanying chart, which illustrates the remarkable orthogenetic accumulation of the fundamental properties and potentialities in the plant kingdom.

SEVERAL PAPERS BEARING ON THE PROBLEMS DISCUSSED.

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